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SCARAB BEETLE COMMUNITIES IN DECIDUOUS DIPTEROCARP AND DRY EVERGREEN FORESTS IN NORTHEASTERN THAILAND*

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INTRODUCTION

Very little is known about tropical insect communities, particularly in the Old World tropics. There have been many studies of the ecology of single species, e.g., on population structure and dynamics of butterflies in Trinidad (EHRLICH & GILBERT, 1973) and on beetles in Costa Rica (JANZEN, 1972) or of small groups of species (e.g., SANDS, 1961 and 1965). But studies on entire insect communities in the tropics are very scarce. CORBET (1941 and 1943 in FISHER, CORBET & WILLIAMS, 1943) studied Malaysian butterfly communities and estimated numbers of individuals in each species, but no further studies on the community structure have been done. JANZEN & SCHOENER (1968 and SCHOENER & JANZEN, 1968) studied foliage insect communities from sweep samples in the dry season in Costa Rican forests differing in moisture regimes. They found that foliage insects in the moister site had larger numbers of individuals and species and, in general, that the species from drier areas or from forests with longer growing seasons had larger body sizes.

The staff of the Centre for Thai National Reference Collections, of which I was a part, had made large collections of insects from two immediately adjacent and differing forests in northeastern Thailand over a long collecting period. These collections allowed me to study the characteristics of these insect communities and to examine the effects of differences in forest structure and microclimate.

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The total collections include tens of thousands of individuals by estimate and an unknown but very large number of species of many insect orders. As a matter of practical necessity, I chose a single group, the scarab beetles, for this study.

Scarab or lamellicorn beetles (if one includes Lucanidae and Passalidae) constitute one of the largest superfamilies of Coleoptera. They are numerous in both species and individuals which makes them interesting for ecological and statistical analysis. They have been the subjects of systematic study and are among the best known superfamilies in Southeast Asia. Certain species have caused damage to crops; for example, larvae of *Anomala siamensis* have destroyed sugar cane plantations in India (ARROW, 1910). Consequently there may be a practical benefit in studying them. Since this insect group includes three trophic types, the lamellicorns might also be useful in predicting distribution of other insect groups that feed on similar food sources.

DESCRIPTION OF ENVIRONMENTS

The collections were made at the "Sakaerat Experiment Station" under the administration of the Applied Scientific Research Corporation of Thailand. This is a forest preserve of about 80 square km situated at 14°30'N, 101°55'E and is about 60 km south of Nakhon Ratchasima (the closest large town) and approximately 300 km northeast of Bangkok (see Fig. 1). Data on the description of environments, if not otherwise cited, are from the reports of the Applied Scientific Research Corportion of Thailand.

The station lies on the foothills adjacent to the Khorat Plateau. Three major different environments occur in and around the Sakaerat Experiment Station : dry evergreen forest, deciduous dipterocarp forest, and agricultural areas. Only the first two environments are involved in this study. The dry evergreen forest is at an elevation of 500 m, and the deciduous dipterocarp forest at 340 m. For simplicity, the former will be referred to as "evergreen forest" and the latter as "deciduous forest" in most of this paper.

Vegetation Dry evergreen forest has a fragmented distribution in Thailand and exists only in restricted areas of the southern, western, eastern, and northeastern sections of the country (WILLIAMS, 1967).





General view of deciduous dipterocarp forest in wet season (upper), August 1969, and in dry season after fire (lower), January 1969 (Photographs courtesy of T. Santisuk)

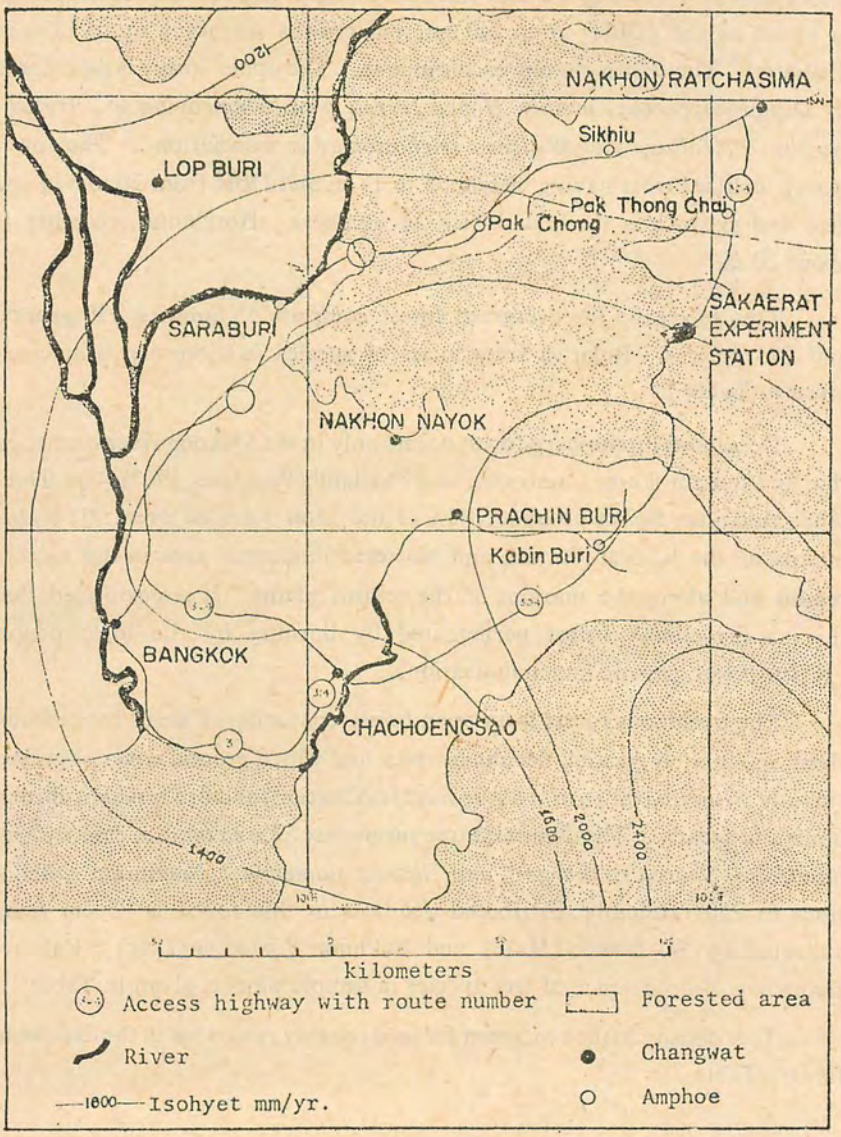


Figure. 1. Location of Sakaerat Experiment Station, northeastern Thailand, showing access highways, isohyets, and forested areas (from ASRCT, 1967).

The evergreen forest at Sakaerat consists of two storeys of trees and undergrowth. The upper storey trees have heights from 20 to 35 m, diameters at breast height (DBH) up to 140 cm, and crowns spreading up to 18 m in diameter. The crown canopy is continuous. The upper storey is dominated by Dipterocarpaceae, mainly *Hopea ferrea*, with *Memecylon* sp., *Hydnocarpus ilicifolius*, and *Walsura trichostemon* in association. The lower storey includes trees having heights 5 to 17 m and DBH from 30 to 140 cm. The undergrowth is thick and rich in climbers. Horizontal visibility is about 20 m.

Tree species in the evergreen forest comprise 55 families, 120 genera, and 175 species. Relative frequencies of species in a one-ha sample are given in Table 1.

Deciduous dipterocarp forest occurs only in the Mekong river countries, that is, Vietnam, Laos, Cambodia, and Thailand (WILLIAMS, 1967). In Thailand, this type makes up about 45% of the total forested area. It occurs mainly on the Khorat Plateau and scattered in a small area in the eastern region and along the margins of the central plains. It is postulated that this is a fire-climax forest perpetuated by burning by the local people (T. SMITINAND, personal communication).

The deciduous forest is an open forest consisting of small to medium-sized, moderately spaced, deciduous trees, and with a ground cover of grasses (mainly *Arundinaria pusilla* at the Sakaerat Station) and fire resistant shrubs, herbs and cycads. The dominant tree species are *Shorea obtusa, Pterocarpus parvifolia, Shorea roxburghii, and Shorea siamensis.* Maximum DBH of trees in 250 randomly distributed quadrats in this forest is 95 cm (data collected by W. Ronald HEYER and Sukhum PONGSAPIPATANA). Relative frequency of occurrence of tree species in sample plots is given in Table 1.

Tree density in the evergreen forest is roughly twice that in the deciduous forest (Table 2).

Table 1. Percentages of individuals of tree species occurring in 114 random samples of 10×10 m quadrats in one square km in deciduous dipterocarp forest, and in one ha quadrat in dry evergreen forest at Sakaerat Experiment Station, northeastern Thailand. Only treess with diameter at breast height 5 cm are included.

Deciduous Dipterocarp Forest		Dry Evergreen Forest	
Tree species	Percentages of individuals		Percentages of individuals
Shorea obtusa	44.79	*Memecylon* sp.	20.09
Pterocarpus parvifolia	10.70	*Hopea ferrea*	19.82
Shorea roxburghii	7.32	*Hydnocarpus ilicifolius*	12.11
Shorea siamensis	4.23	*Walsura trichostemon*	10.35
Quercus mespilifolioides	2.82	*Aglaia pirifera*	7.37
Xylia kerrii	2.82	*Canthium brunnescens*	5.26
Sindora siamensis	2.54	*Syzygium cumini*	3.51
Adina cordifolia	1.97	*Linociera microstigma*	1.84
Gardenia coronaria	1.41	*Litsea chinensis*	1.76
Berrya sp.	1.13	*Lagerstroemia calyculata*	1.49
Dalbergia bariensis	1.13	*Randia wittii*	1.49
D. oliveri	1.13	*Unidentified*	1.31
Diospyros sp.	1.13	*Melodorum fruticosum*	1.14
Irvingia malayana	1.13	*Grewia paniculata*	1.05
Buchanania reticulata	0.84	*Anisoptera oblonga*	0.96
Careya arborea	0.84	*Eriobotrya bengalensis*	0.88
Grewia paniculata	0.84	*Horsfieldia irya*	0.79
Hymenodictyon excelsum	0.84	*Saprosma latifolium*	0.79
Morinda coreia	0.84	*Ixora* sp.	0.70
Bauhinia variegata	0.56	*Shorea henryana*	0.70
Cordia obliqua	0.56	*Mammea siamensis*	0.61
Diospyros ehretioides	0.56	*Walsura* sp.	0.61
Dipterocarpus obtusifolius	0.56	*Dialium cochinchinense*	0.53
Garuga pinnata	0.56	*Pterospermum diversifolium*	0.53
Schleichera oleosa	0.56	*Phoebe* sp.	0.44
Symplocos sp.	0.56	*Mitrephora vandiflora*	0.35

Table 1. (Cont.)

Deciduous Dipterocarp Forest		Dry Evergreen Forest	
Tree species	Percentages of individuals		Percentages of individuals
Urena lobata	0.56	*Streblus taxoides*	0.35
Vitex pinnata	0.56	*Mallotus* sp.	0.26
Annonaceae	0.56	*Anogeissus acuminata*	0.17
Albizia procera	0.28	*Anthocephalus chinensis*	0.17
A. lebbeck	0.28	*Gmelina asiatica*	0.17
Antidesma sp.	0.28	*Irvingia malayana*	0.17
Butea monosperma	0.28	*Siphonodon celastrineus*	0.17
Canarium subulatum	0.28	*Trigonostemon* sp.	0.17
Casearia grewiifolia	0.28	*Antiaris toxicaria*	0.09
Croton obongifolius	0.28	*Antidesma* sp.	0.09
Dalbergia cultrata	0.28	*Ardisia helferi*	0.09
Dillenia ovata	0.28	*Baccaurea* sp.	0.09
Erythrophloeum succirubrum	0.28	*Cananga latifolia*	0.09
Lagerstroemia floribunda	0.28	*Canarium subulatum*	0.09
L. macrocarpa	0.28	*Chaetocarpus castanocarpus*	0.09
Parinari annamense	0.28	*Cinnamomum iners*	0.09
Pevetta sp.	0.28	*Chrysophyllum roxburghii*	0.09
Phyllanthus emblica	0.28	*Cratoxylon* sp.	0.09
Polyalthia sp.	0.28	*Diospyros montana*	0.09
Salmalia insignis	0.28	*Diospyros* sp.	0.09
Strychnos nux-vomica	0.28	*Euphorbia* sp.	0.09
Terminalia tripteroides	0.28	*Garcinia speciosa*	0.09
T. bellirica	0.28	*Parkia streptocarpa*	0.09
Wendlandia tinctoria	0.28	*Sterculia* sp.	0.09
		Syzygium gratum	0.09
Total number of tree species:	51	*Tarenna* sp.	0.09
Total number of tree individuals:	356	*Terminalia tripteroides*	0.09
		Vitex quinata	0.09
		Xerospermum intermedium	0.09
		Total number of tree species:	56
		Total number of tree individuals:	1,141

Table 2. Woody vegetation (DBH≥ 1 cm) in deciduous dipterocarp forest and dry evergreen forest at Sakaerat Experiment Station, north-eastern Thailand. Samples based on 100 randomly distributed 25 × 25 ft (58.06m²) quadrats in each forest (INGER and COLWELL, in ms.)

	Deciduous dipterocarp forest		Dry evergreen forest	
Plant DBH (cm)	Number of trees	Density per 100 m²	Number of trees	Density per 100 m²
<5	165	2.84	531	9.15
5–20	399	6.87	784	13.50
>20	118	2.03	137	2.36
All woody plants	682	11.75	1,452	25.01

Soil and Floor Structure Soil in the evergreen forest, which is at a higher altitude, is a mixture of shale and sandstone; soil in the deciduous forest is mostly derived from pure sandstone. Soils under the deciduous forest are generally more shallow and stony. In the deciduous forest, many large stones lie more or less on the surface, whereas in the evergreen forest they are mostly imbedded in the soil. The reason for this difference is probably that more sheet erosion occurs in the deciduous forest because of its open nature. The surface soil of the deciduous forest is sandier and less humid than that of the evergreen forest.

In the deciduous forest, low soil moisture content (SANDHAGUL & KLINSUKONT, 1971), high evaporation (see p. 50), and sandier soil may be less favourable to the oviposition of scarabs and to the development of larvae. In *Phanaeus* (Coprini) less sand in the soil stimulates adults to build more brood balls and the sandier the soil, the fewer larvae survive (FINCHER, 1973).

Differences between the two forests in types of floor cover are clearly demonstrated in Table 3. Grass, which is the major floor cover in the unburned deciduous forest, never occurs in the evergreen forest. Most of the floor of the evergreen forest was covered by dead leaves or litter 1–3 cm

thick. The drastic influence of fire on floor cover in the deciduous forest can also be seen in Table 3. OGAWA *et al.* (1961) estimated that, in deciduous forest, fire reduced the total supply of organic matter about two-thirds.

Table 3. Percentages of floor covered by indicated structural types along transects in two forests at Sakaerat Experiment Station, north-eastern Thailand. Data Collected on April 14-16, 1969 (INGER & COLWELL,)

Floor structural type	Dry evergreen forest	Deciduous dipterocarp forest	
		Unburned	Burned
Grasses	0	53.5	37.3
Dead leaves	97.6	35.0	14.5
Rocks	0	11.3	18.4
Logs	0.8	0.2	2.5
Bare soil	1.2	0	26.9
Tree roots	0.4	0	0.4
Total meters	90	30	90

Climate Climate in the Sakaerat area is under the control of monsoon winds, as is generally the case with other regions of Thailand. The northeast monsoon wind influences the dry or cool season, the southwest wind causes the rainy season (WILLIAMS, 1967). The relatively long dry season and the nature of soil in the Khorat Plateau make this region the most arid in Thailand.

Precipitation during the study year (January 1969–December 1969), though varying widely between the two forests in total amounts (1490 mm in the deciduous forest and 1003 mm in the evergreen forest), shows a clear seasonal pattern (Fig. 2) of rainfall from March to October with peaks in March, June and September. Precipitation for the years 1941–1960 at Nakhon Ratchasima, the northeast meteorological station, 60 km NNE from Sakaerat, also shows a similar pattern (data courtesy of the Thai Royal Department of Meteorology).

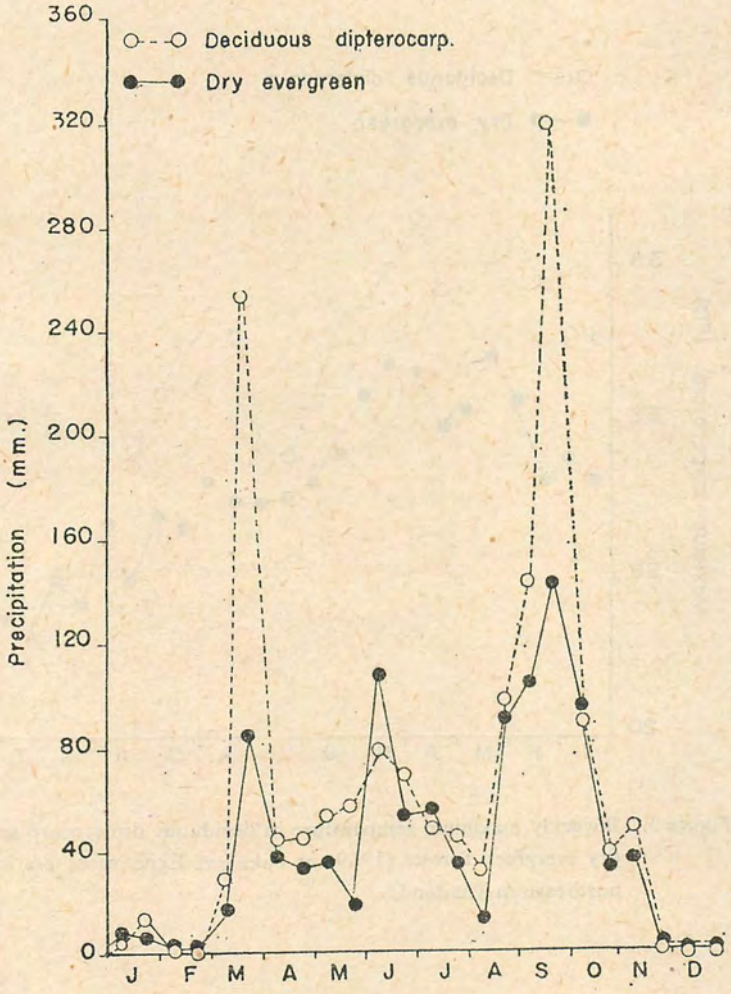


Figure 2. Biweekly total rainfall in deciduous dipterocarp and dry northeastern evergreen forests (1969) at Sakaerat Experiment Station, Thailand.

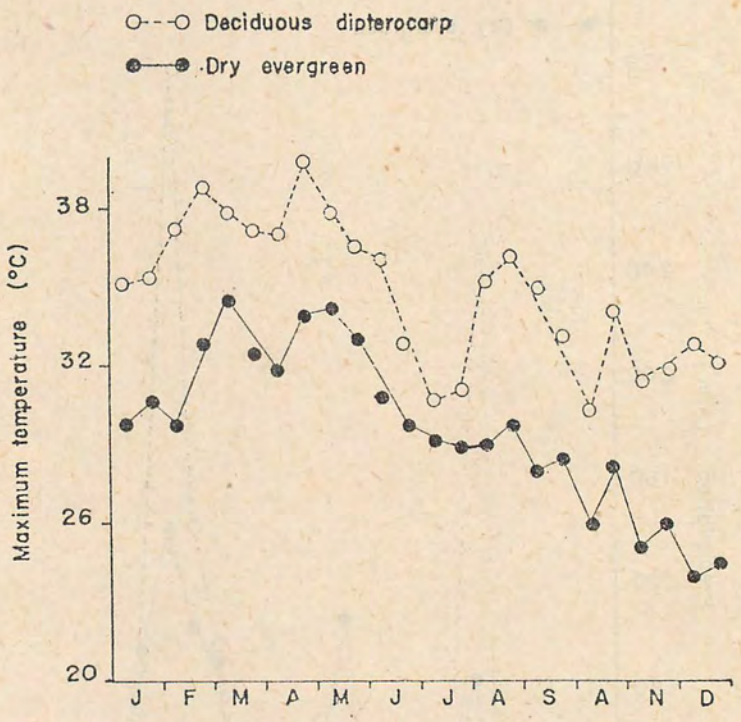


Figure 3. Biweekly maximum temperature in deciduous dipterocarp and dry evergreen forests (1969) at Sakaerat Experiment Station, northeastern Thailand.

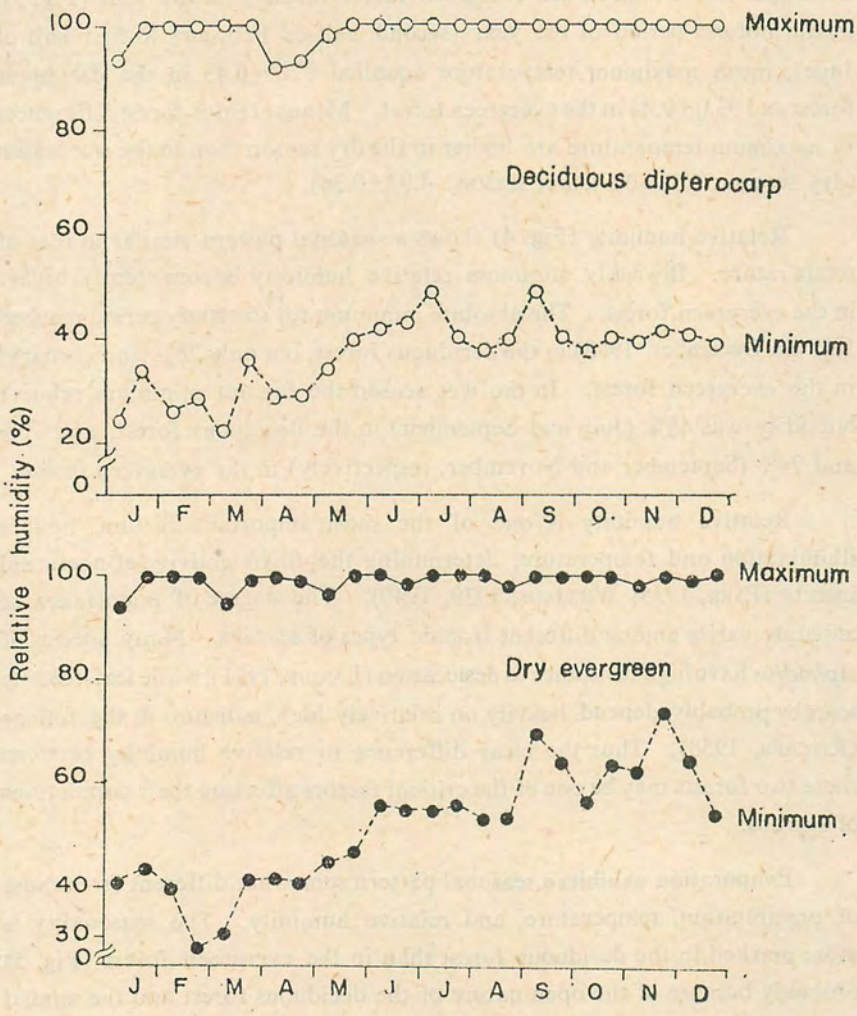


Figure 4. Maximum and minimum relative humidity in deciduous dipterocarp and dry evergreen forests (1969) at Sakaerat Experiment Station, northeastern Thailand.

Biweekly maximum air temperatures are consistently higher in the deciduous forest than in the evergreen forest throughout the year (Fig. 3). In the hottest period of the year (second half of February to first half of June), mean maximum temperature equalled 37.7±0.43 in the deciduous forest and 33.0±0.44 in the evergreen forest. Means of inter-forest differences in maximum temperature are higher in the dry season than in the wet season (dry season : 6.38±0.54, wet season : 4.92±0.36).

Relative humidity (Fig. 4) shows a seasonal pattern similar to that of temperature. Biweekly minimum relative humidity is consistently higher in the evergreen forest. The absolute minimum for the study period reached 18% (in December, 1968) in the deciduous forest, but only 28% (in February) in the evergreen forest. In the wet season the highest minimum relative humidity was 48% (July and September) in the deciduous forest, and 70% and 74% (September and November, respectively) in the evergreen forest.

Relative humidity is one of the most important factors, besides illumination and temperature, determining the flight activity of nocturnal insects (PARK, 1935; WILLIAMS, 1939, 1940). The degree of importance of moisture varies among different trophic types of scarabs. Many species of *Aphodius* have high resistance to desiccation (LANDIN, 1961), while leaf-feeding scarabs probably depend heavily on relatively high moisture in the foliage (RITCHER, 1958). Thus the clear difference in relative humidity between these two forests may be one of the critical factors affecting their populations of scarabs.

Evaporation exhibits a seasonal pattern somewhat different from those of precipitation, temperature, and relative humidity. The seasonality is more marked in the deciduous forest than in the evergreen forest (Fig. 5) probably because of the open nature of the deciduous forest and the annual fire. In the deciduous forest, the period of high evaporation started in the first half of November but continued into the first half of May (dry season by temperature and relative humidity ran from the second half of November to the first half of March). The longer period of high evaporation as compared with low relative humidity may be caused mainly by high wind velocities that persist through the first half of May. Mean wind velocity from the first half of January to the first half of March was 2.7 km/hr, from

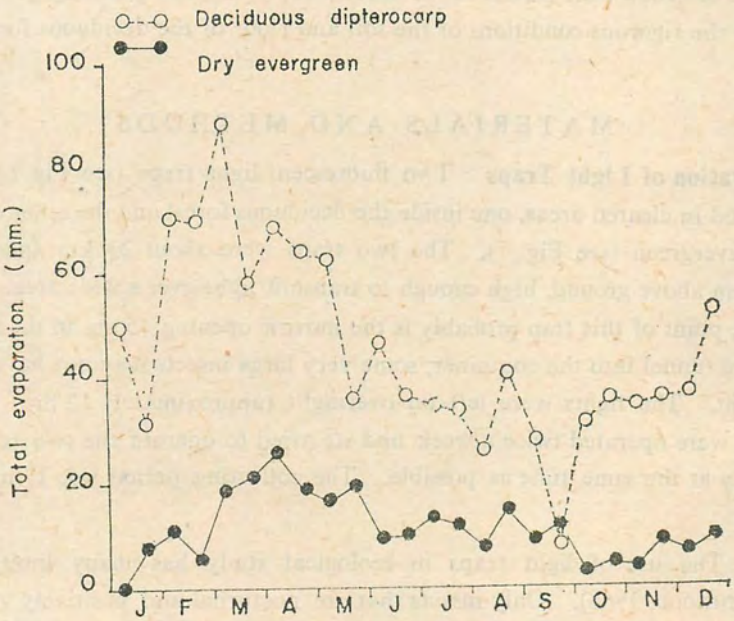


Figure 5. Biweekly total evaporation in deciduous dipterocarp and dry evergreen forests (1969) at Sakaerat Experiment Station, northeastern Thailand.

the second half of March to the second half of May 2.8 km/hr, and from the second half of May to the second half of December 1.5 km/hr. The maximum biweekly total evaporation (Fig. 5) in the deciduous forest was 88.8 mm (first half of March), while the maximum in the evergreen forest was 25.9 mm (first half of April).

As will be shown later, on the basis of these main environmental factors – climate, vegetation, soil and floor structure – probably the deciduous forest is generally less favourable for herbivorous and saprophagous scarabs, but more favourable for coprophagous scarabs than the evergreen forest. Low soil moisture, sandier soil, and annual fire in the deciduous forest are likely to be less favourable for the reproduction of scarabs that oviposit in the soil.

But eggs and larvae of the dung beetles, which mainly oviposit in dung heaps or brood balls (HALFFTER & MATTHEWS, 1966), are partially protected from the rigorous conditions of the soil and floor of the deciduous forest.

MATERIALS AND METHODS

Operation of Light Traps Two fluorescent light traps (see Fig. 6) were located in cleared areas, one inside the deciduous forest and the other one in the evergreen (see Fig. 7). The two traps were about $2\frac{1}{4}$ km apart and 154 cm above ground, high enough to transmit light over a wide area. The weak point of this trap probably is the narrow opening (5 cm in diameter) of the tunnel into the container; some very large insects may not have been caught. The lights were left on overnight (approximately 12 hr). Both traps were operated twice a week and we tried to operate the two traps as nearly at the same time as possible. The collecting period was 17 months long.

The use of light traps in ecological study has many limitations (SOUTHWOOD, 1968). Only insects that are nocturnal and positively phototactic will be caught. Time of flight activity, climatic condition and moonlight affect the yield of the catch (WILLIAMS, 1939 and 1940). The light traps were thus not likely to collect all insects in the area. Therefore, the collection cannot be used for analysis of the entire community. Exact relative abundance of different species cannot be obtained this way. However, light trap collections can be used for comparative studies. Since the traps in the two forests operated under similar limitations, the collections are susceptible to similar sources of bias and provide interesting comparative data from the two forest communities.

Handling of Specimens Specimens were dried and sorted out to order in the laboratory of the Applied Scientific Research Corporation of Thailand in Bangkok. When the Coleoptera collections arrived at the Field Museum, I fumigated, relaxed and sorted out only lamellicorn beetles. Individuals that apparently represented different species were mounted for identification. Since there may be sibling species that I was unable to distinguish in several genera (e.g., *Serica*), the numbers of species listed here represent minimum estimates. Although all of the beetles could be placed into described genera,

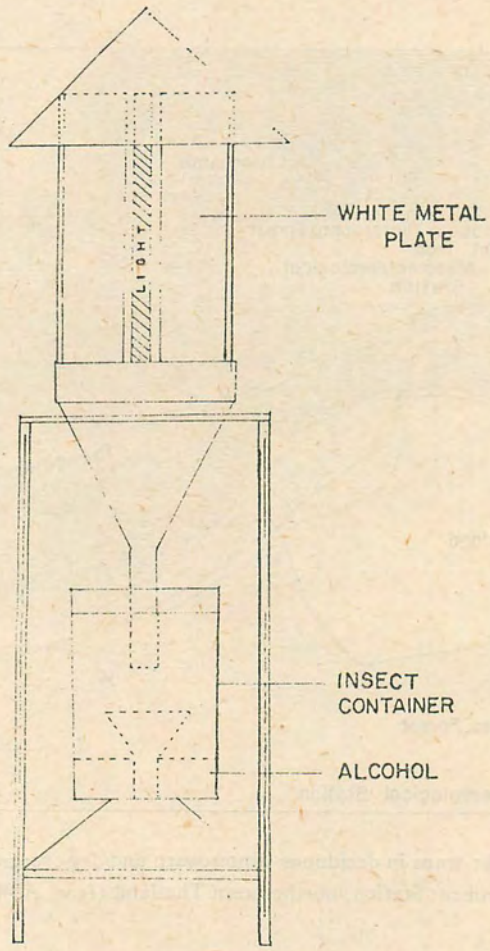


Figure 6. Light trap used in collecting insects at Sakaerat Experiment, Station, northeastern Thailand.

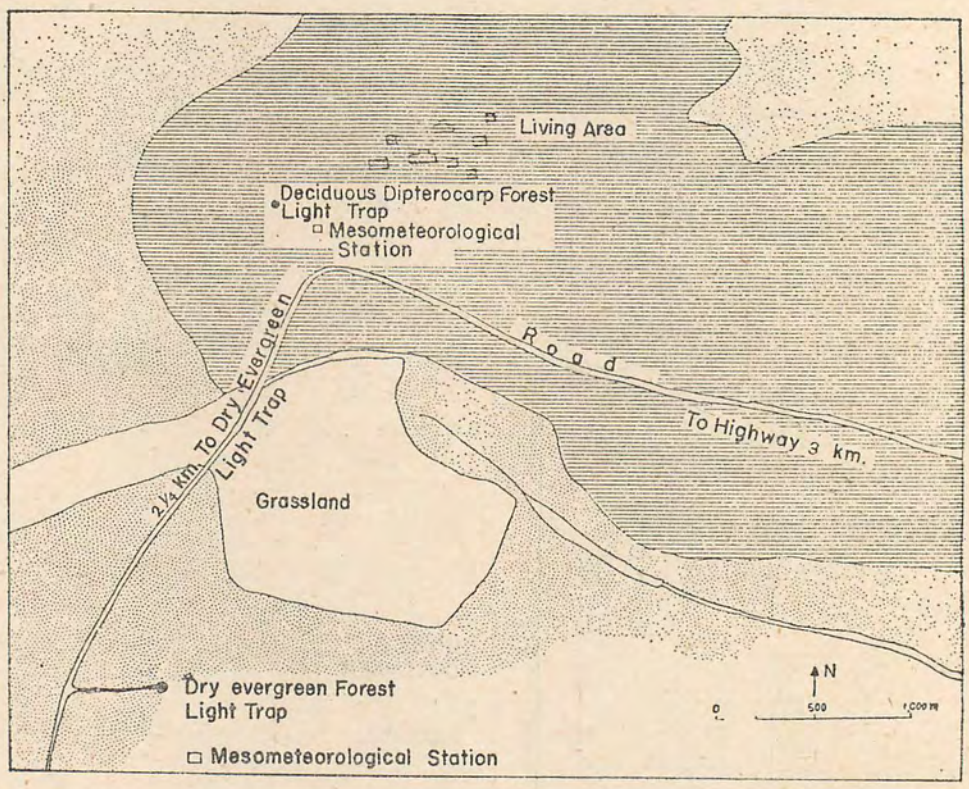


Figure 7. Location of light traps in deciduous dipterocarp and dry evergreen forests at Sakaerat Experiment Station, northeastern Thailand (from ASRCT, 1967).

in some cases it was not possible to determine the species name. In such instances, I designated these species by number, for example, *Aphodius* sp. #1. In a number of genera consisting of very similar species, the male genitalia, which are diagnostic, were dissected out and compared to distinguish the species. I used this technique with *Anomala, Serica, Phyllophaga.*

Scarab beetles were measured from the apex of the clypeus to the end of the pygidium with a ruler. In some cases small species were measured under a dissecting microscope.

For the analysis of species mean lengths it was essential to obtain exact lengths; I therefore measured only unbroken specimens. On some collecting nights large numbers of individuals of a single species were caught. Large series comprising more than 20 undamaged individuals were subsampled randomly to select individuals for measurement.

Aliquots of the Total Collections The traps were in operation 88 nights, yielding an enormous number of insects. Even restricting the study to scarabs still leaves a very large sample. To bring the numbers of individuals to be identified and measured to a manageable size, 32 samples (a sample being the lamellicorn beetles of one collecting night) were chosen at random from the deciduous forest, using a table of random numbers. With four exceptions, there were samples collected on the same nights in the evergreen forest. In the four cases in which precisely matched sample pairs did not exist, I selected the evergreen forest sample closest to the corresponding collecting night in the deciduous forest. The actual sample nights are listed in Appendix I. The 32 pairs of samples were distributed in dry and wet seasons and consisted of 1,374 and 1,883 individuals from the deciduous and the evergreen forests, respectively.

DATA AND ANALYSIS

Taxonomic Composition and Species Overlap

Differences in abundance among species For both environments, the plot (Fig. 8) of numbers of species against numbers of individuals describes an approximate hyperbolic curve of the type proposed by WILLIAMS, *et al.* (1943). A few common species are represented by large numbers and many

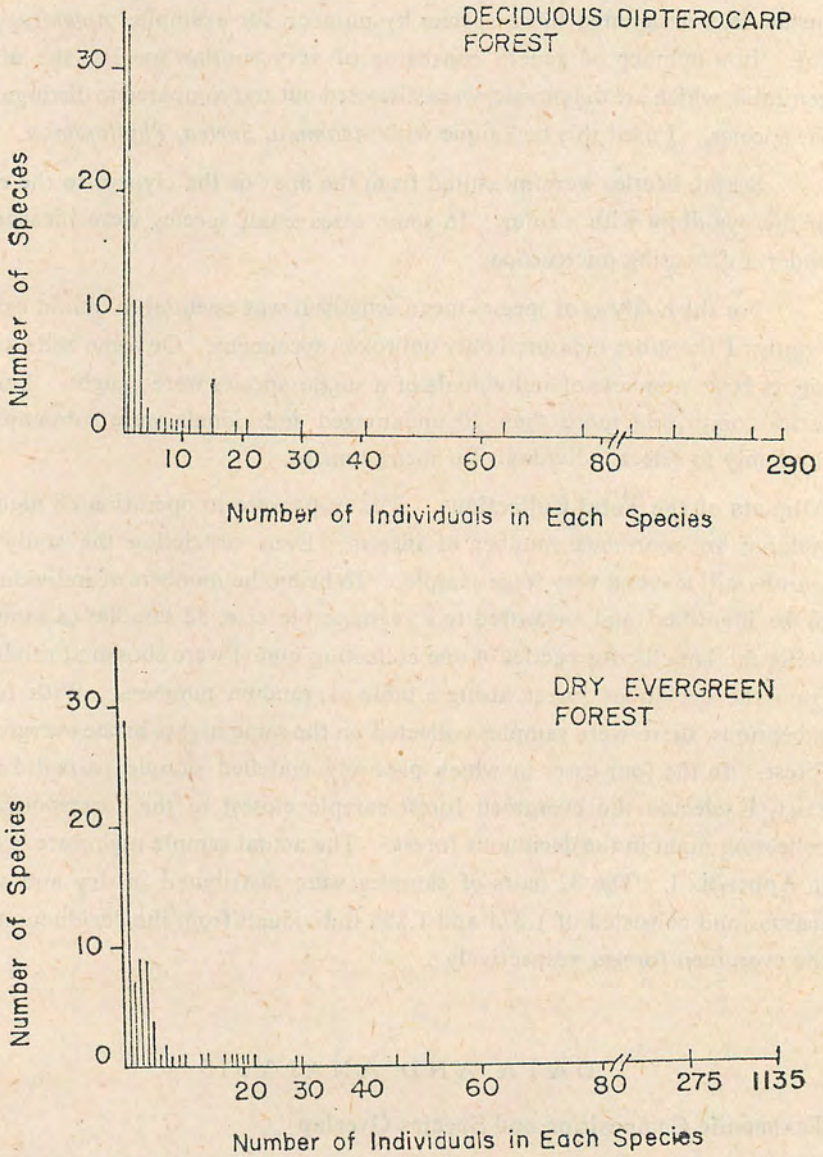


Figure 8. Abundances of individuals within species of scarab beetles in deciduous dipterocarp and dry evergreen forests at Sakaerat Experiment Station, northeastern Thailand

more rare species by only a few individuals. In the deciduous forest, 1,374 individuals were distributed among 83 species, and in the evergreen forest, 1,883 individuals represented 78 species.

In both forests, almost two-thirds of the species were very rare (1–5 individuals per species), and the remaining one-third were divided equally between relatively rare (6–16 individuals per species) and abundant species (17 or more individuals per species).

In the evergreen forest, most of the individuals (1,047 out of 1,135) of *Anomala* sp. ♯2, the most abundant species, occurred in one sample, probably because of a mass emergence in a short interval.

Taxonomic composition. The lamellicorn beetles are one of the largest groups of the Coleoptera; so far as we now know there are about 2,000 species in the area covered by India, Pakistan, Burma and Ceylon (ARROW, 1910) and about 19,300 species throughout the world (ARNETT, 1968). Most of the lamellicorn families and subfamilies covered by this study are world-wide in distribution except the Passalidae, which are not found in Europe. In general, the lamellicorn genera represented in this study are widely distributed in southern, southeastern, and eastern Asia, the East Indies and Australia (ARROW, 1910). Some like *Onthophagus* and *Anomala* are essentially world-wide.

The taxonomic composition of the scarab communities from the two forests at Sakaerat is generally similar. (Species lists of these two forest samples are given in Appendix II). The 83 species in the deciduous forest represent 22 genera in three families and eight subfamilies, and the 78 species in the evergreen forest represent 27 genera in three families and eight subfamilies. Two families, Lucanidae and Passalidae, are very rare in both forests (Table 4). In both forests, the major family, Scarabaeidae, comprises eight subfamilies. The more common subfamilies in both forests, in terms of numbers of species, were the Melolonthinae, Rutelinae, Aphodiinae and Coprinae. The family Scarabaeidae contributed 97% of the species in the deciduous forest and 89% of those in the evergreen. The percentages of each major subfamily were roughly similar in both forests. The rare family, Lucanidae, had more species in the evergreen than in the deciduous forest. No species of Euchirinae occurred in the samples from the deciduous, while no species of the Geotrupinae occurred in the samples from the evergreen forest (see Table 4).

Table 4. Taxonomic composition of the scarab communities in deciduous dipterocarp and dry evergreen forests at Sakaerat Experiment Station, northeastern Thailand. All samples are included.

Taxa	Deciduous dipterecarp forest			Number of common species	Dry evergreen forest			Total species at Sakaerat
	No. of species	Percentage of total	No. of exclusive species		No. of species	Percentage of total	No. of exclusive species	
LUCANIDAE	2	2	0	2	6	8	4	6
PASSALIDAE	1	1	0	1	2	3	1	2
SCARABAEIDAE	80	97	48	32	70	89	38	118
Ochodaeinae	1	1	0	1	1	1	0	1
Hybosorinae	1	1	0	1	1	1	0	1
Dynastinae	3	3	2	1	4	5	3	6
Euchirinae	0	0	0	0	1	1	1	1
Geotrupinae	2	2	2	0	0	0	0	2
Aphodiina	13	15	7	6	10	13	4	17
Coprinae	9	11	5	4	7	9	3	12
Rutelinae	14	20	9	5	16	21	11	25
Melolonthinae	37	44	23	14	30	38	16	53
Subtotal	80	97	48	32	70	89	38	118
TOTALS	83	100	48	35	78	100	43	126

Species overlap between forests I analyzed species overlap using two approaches : (1) enumeration of species and (2) an index of overlap (HORN, 1966).

There were 35 species common to the two communities, which amounts to 42% of the species in the deciduous forest and 45% of those in the evergreen. The percentage of species overlap between forests is relatively low and is roughly the same in each major subfamily (percentage in the deciduous forest is given first) ; Melolonthinae : 38%, 47%; Rutelinae : 36%, 31%; Aphodiinae : 46%, 60%, and Coprinae : 44%, 57%. These four major subfamilies are widely distributed in tropical Asia.

Considering that the two forests are immediately adjacent to one another, it is not impossible that individuals may have dispersed from their "proper" forest and became accidentally trapped in the "wrong" forest. If it were possible to eliminate such transient species from the species list of each habitat, this would lower the overlap even further.

The assignment of species to a particular environment is meaningless for those that have only 1–3 individuals in both communities. More than 16 individuals in one or both forests constitutes a reliable enough sample. Any of these abundant species ($N \geq 17$) may be classified as preferring one habitat or the other if its numbers in one forest are at least three times its numbers in the other (see Fig. 9). On this basis, six species–*Onthophagus* sp. ♯1, *Serica* sp. ♯14, *Phaeochrous emarginatus*, *Rhyssemus germanus*, *Ochodaeus* sp. ♯1 and *Serica* sp. ♯10 prefer the deciduous, while five species–*Anomala* sp. ♯2, *Xylotrupes gideon*, *Apogonia* sp. ♯1, *Cyphochilus proximus*, and *Anomala* sp. ♯5 prefer the evergreen forest. Thus, of the 14 common species of scarabs occurring in both communities, only 3 are approximately equally abundant in both forests.

I used HORN's (1966) equation

$$R_o = \frac{\sum_i (x_i + y_i) \log (x_i + y_i) - \sum_i x_i \log x_i - \sum_i y_i \log y_i}{(X + Y) \log (X + Y) - X \log X - Y \log Y}$$

which is based on SHANNON–WIENER information theory, as an appropriate index overlap. Here x_i and y_i are characteristic samples of each species from total sample populations X and Y of all species, respectively. That

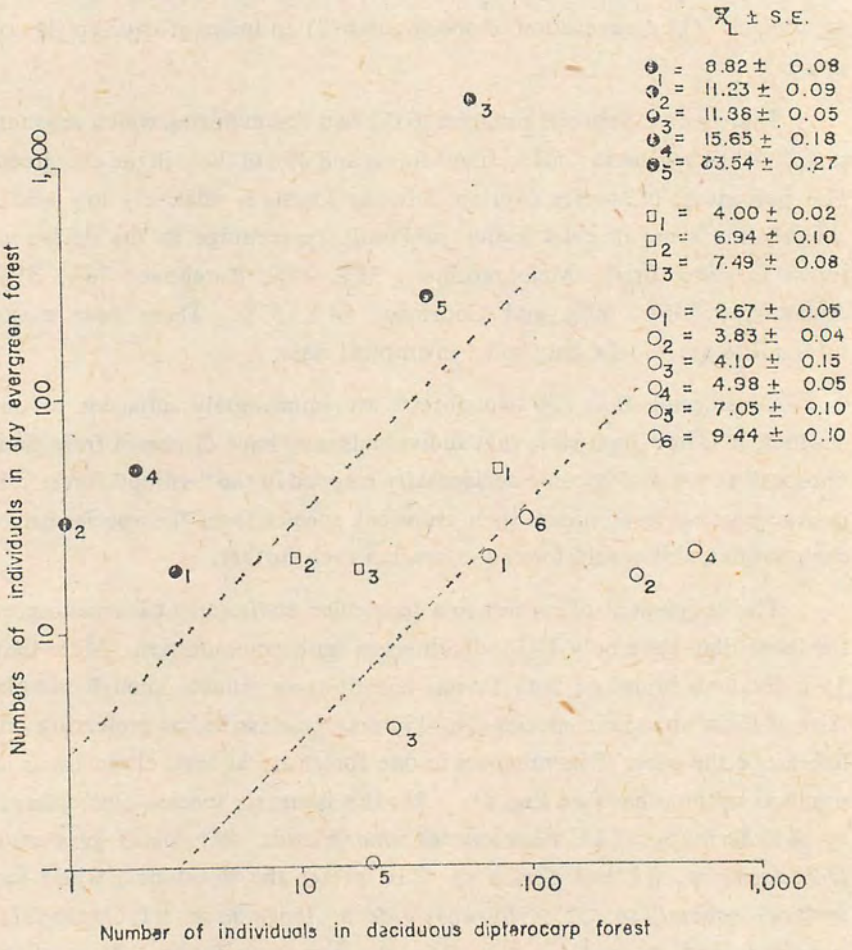


Figure 9. Relative abundances within environments of species of scarab beetles occurring in both forests at Sakaerat Experiment Station. Sample size of each species ≥ 17. Species mean length (mm) given in inset. Predominant distribution based on ratios $\geq 3:1$ (above upper and below lower dashed lines). Predominantly evergreen forest species (solid circles) : 1=*Apogonia* sp. ♯1, 2=*Anomala* sp. ♯5, 3=*Anomala* sp. ♯2, 4=*Cyphochilus proximus*, 5=*Xylotrupes gideon*. Predominantly deciduous forest species (open circles) : 1=*Rhyssemus germanus*, 2=*Onthophagus* sp. ♯1, 3=*Ochodaeus* sp. ♯1, 4=*Serica* sp. ♯14, 5=*Serica* sp. ♯10, 6=*Phaeochrous emarginatus*. Approximately equally abundant in both forests (open squares) : 1=*Aphodius* sp. ♯3, 2=*Serica* sp. ♯1, 3=*Serica* sp. ♯5.

is, species i is represented x_i times in collection X and y_i times in collection Y. The value of the index of overlap between evergreen and deciduous communities is 0.0015, which is very low, as this index ranges between 0.0 to 1.0.

Trophic Types of the Scarab Beetles I classify the adult scarab beetles into three main trophic types : herbivores, coprophages and saprophages. The herbivores feed on foliage, the coprophages on animal dung, and the saprophages on decaying leaves and other plant materials. Assignment of food habits is based on ARROW (1910, 1917, 1931 and1949), PAULIAN (1945, 1959), BALTHAZAR (1964), and RITCHER (1958).

In general all species of Geotrupinae, Aphodiinae and Coprinae for which food habits are known are coprophages. The majority of species of Ochodaeinae, Hybosorinae, Dynastinae and Euchirinae for which food habits are known are saprophages. Lucanidae and Passalidae are also classified as saprophages (ARROW, 1949). The remaining subfamilies, Rutelinae and Melolonthinae, are known to be herbivores.

Even though the larval food is as important as food for the adult stage, only the adult trophic types are considered in this analysis since there is more reliable information for adults. There are some plant feeders among the larvae of the lamellicorn coprophages and saprophages and some dung feeders and scavengers among the larvae of the herbivores (RITCHER, 1958). However, it is evident that the majority of the larvae of the dung feeders and saprophages have food habits similar to their adults, and the majority of root-feeding larvae belong to herbivorous adults. One exception is *Xylotrupes gideon;* its larvae are root-feeders but the adults are saprophages.

I analyzed the abundance of the trophic types in two ways. The first is based on species richness and the number of individuals in the total samples (Table 5). The second approach is based on the ratio of individuals and rank of abundance within samples (Table 6).

Comparison of the two communities In both forests, species richness is greatest among the herbivores, intermediate in the coprophages and least in the saprophages (last column of Table 5). In the deciduous forest, the species richness of coprophages is much higher than that of saprophages, whereas in the evergreen forest these two trophic types are nearly equal.

The rank of trophic types in number of individuals remains the same as species richness in the deciduous forest (Table 5, last column). In the evergreen forest, the herbivores remain the most abundant, but the saprophages outnumber the coprophages.

As measured both by species richness and numbers of individuals, saprophages are more abundant in the evergreen forest than in the deciduous. This is not surprising since the evergreen forest produces more woody litter which is not burned and the lower evaporation and more moderate temperatures promote plant decaying activity of fungi. The rate of cellulose decomposition in the soil by fungi is known to be higher in the evergreen forest than in the deciduous (SANDHAGUL & KLINSUKONT, 1971).

Table 5. Seasonal distribution of species richness and numbers of numbers of individuals (in parentheses) of three trophic types of scarab beetles in two forest types at Sakaerat Experiment Station, north-eastern Thailand.

	1968	1968-69	1969		
	Wet season	Dryseason	Wet season		
Trophic type	Second half (5 samples)	(11 samples)	First half (8 samples)	Second half (8 samples)	Total
Deciduous dipterocarp forest					
Herbivore	5 (162)	7 (12)	46 (486)	11 (50)	53 (710)
Coprophage	5 (109)	6 (120)	11 (87)	12 (112)	22 (428)
Saprophage	3 (16)	4 (52)	7 (137)	4 (31)	8 (232)
Dry evergreen forest					
Herbivore	7 (64)	18 (31)	39 (1347)*	11 (11)	52 (1453)*
Coprophage	3 (22)	4 (31)	7 (21)	7 (12)	15 (86)
Saprophage	6 (50)	6 (118)	6 (228)	5 (48)	11 (344)

* If we eliminate *Anomalo sp.* ‡2 which was represented by 1,047 individuals in one sample, the number of the remaining herbivores in the first half of the wet season will be 300.

Table 6: Seasonal variation in proportions of abundance and frequencies of dominance (most abundant type in a sample; shown in parenthesis) of three trophic types of scarabs within samples in two forest types at Sakaerat Experiment Station, northeastern Thailand. Samples of the dry and the second half of wet season are pooled from both 1968 and 1969. Dominance was not calculated for 6 samples which lacked scarabs.

Trophic type	Dry season (11 samples)	Wet season		X±SE
		First half (8 samples)	Second half (13 samples)	
Deciduous dipterocarp forest				
Herbivore	0.18 (1.5)	0.46 (4)	0.28 (3)	0.30±0.05
Coprophage	0.62 (5)	0.21 (0)	0.56 (8)	0.48±0.06
Saprophage	0.20 (1.5)	0.33 (4)	0.16 (1)	0.22±0.03
Dry evergreen forest				
Herbivore	0.51 (5)	0.67 (8)	0.34 (3.5)	0.48±0.07
Coprophage	0.34 (3)	0.06 (0)	0.19 (4)	0.20±0.05
Saprophage	0.15 (1)	0.27 (0)	0.47 (5.5)	0.32±0.06

In the deciduous forest, the coprophages rank first both in mean of within sample proportions and in dominance within samples (Table 6), closely followed by the herbivores and the saprophages. Herbivores and saprophages are somewhat similar in both measures. The dominance of coprophages in these measures despite the predominance of herbivores in the pooled sample may indicate that fluctuation of abundance from sample to sample is greater in herbivores. That such a pattern does not occur in the evergreen forest may reflect the stronger influence of seasonality in the deciduous forest.

Seasonal abundance of different trophic types Since these light trap data are based on only 16 months of observation, they are probably not sufficient to draw a definitive picture of seasonal patterns. But for a comparative study of the scarab populations in both forests, the data are strongly suggestive.

In terms of species richness (Table 5) coprophages are least numerous in the dry season and roughly constant in the two halves of the wet season

in both communities. Saprophages maintain a roughly constant level in all three periods in the evergreen forest, but are distinctly more numerous in the first half of the wet season in the deciduous forest. Herbivores are conspicuously more numerous in the first half of the wet season in both communities, but especially so in the deciduous forest.

In terms of number of individuals (Table 5), herbivores and saprophages reach peaks of abundance in the first half of the wet season in both communities. The herbivores in the evergreen forest at that time are mostly of one species, *Anomala* sp. #2. But even if we remove the 1,047 individuals of that species caught in one sample, the seasonal pattern of herbivores remains unchanged. Coprophages reached their peaks of individual abundance in both forests during the dry season in spite of reduced species richness at that time.

In terms of mean sample proportions and frequency of dominance within samples (Table 6), in the deciduous forest coprophages are the dominant trophic group in the dry season and in the second half of the wet season whereas herbivores predominate in the first half of the wet season. In the evergreen forest, herbivores are dominant in the dry season and in the first half of the wet season, whereas saprophages are dominant in the second half of the wet season.

At least some of these seasonal variations are probably related to the quantity and quality of food supply. Presumably the virtual absence of green leaves in the deciduous forest during the dry season acts as a very strong selective force inhibiting activity of herbivorous scarabs, which emerge in great numbers in the first half of the wet season with the flush of new leaves. Since green leaves are present throughout the year in the evergreen forest, we would expect roughly equal emergence of herbivorous species in all seasons—if simple availability of green leaves were the controlling factor. However, the situation is clearly not that simple as herbivores are distinctly more numerous early in the wet season (Table 5) than at other times. If the quality of the green vegetation is superior early in the wet season, herbivorous species might be responding to that factor, and this might explain the decline in numbers of herbivores in the second half of the wet season relative to the preceding period in both forests. A qualitative difference in the food supply might also provide the explanation for greater abundance of herbivores

in the dry season than in the second half of the wet season in the evergreen forest : species that emerge slightly in advance of the best food supply may be in a better position to use that resource than ones that emerge after the first appearance of that supply.

Saprophages were more active and more numerous in the wet season, when presumably the rate of plant decay is higher. Coprophages differ from the other trophic types in being relatively active during the dry season : In that period their abundance as individuals was highest, their proportions within samples were highest, and their dominance within samples was relatively high. These characteristics suggest that suitable dung may be more available in dry circumstances, which may be related to a reduced rate of bacterial activity. MADLE (1934, cited in LANDIN, 1961, p. 192) stated that bacteria change dung-dissolved albumen into "bacterial" albumen which is mostly unfavouraele to adults and larvae of coprophagous scarabs because of specific enzymatic properties. It is possible that this bacterial activity is lower in the deciduous forest than in the evergreen because of the generally lower humidity in the former most of the year. Reduced bacterial activity may allow a dung heap to remain in suitable condition for coprophagous scarabs longer. This factor may account for the greater abundance and greater species richness of coprophages in the deciduous forest as well as their seasonal patterns just mentioned.

Unfortunately, there is no adequate information comparing abundance of mammals in these two forests so that we do not know if more dung is produced in one forest. Mammals that commonly occur are rabbits, rats, squirrels, etc. (unpublished study of Applied Scientific Research Corporation of Thailand); there were no cattle in either forest at the time of collection of the beetle samples.

Seasonal patterns of species Herbivorous species are relatively seasonally restricted insects in both environments. In the deciduous forest, eight abundant herbivorous species occurred exclusively in the wet season (see Figs. 8 and 9), and no species was collected in all seasons.

Two species, *Anomala* sp. ♯2 and *Adoretus* sp. ♯14, were observed only in the early wet season. In the evergreen forest, four out of seven abundant herbivorous species, *Anomala* sp. ♯2, *Anomala* sp. ♯5, *Serica* sp.

#1, and *Serica* #14, were trapped exclusively in the first half of the wet season; one species, *Cyphochilus proximus*, only in the second half of the wet season; and two species, *Serica* sp. #5 and *Apogonia* sp. #1, in both wet and dry seasons. Another herbivore of the evergreen forest, the relatively rare species, *Serica* sp. #6, was also caught in all seasons.

Although only the evergreen forest had herbivores that were active in all seasons, these three species, *Apogonia* sp. #1, *Serica* sp. #5 and *Serica* sp. #6, occurred in both forests. The differences between the seasonal distributions of these species in the two forests may be another effect of the difference between the forests in availability of green leaves in the dry season.

Although coprophages are present throughout the year in the deciduous forest, only two species, *Onthophagus* sp. #1 (Fig. 9) and *Copris furciceps*, occurred throughout the three seasons. These two species, though present in the evergreen forest, were not found there in the dry season. The suggested difference between the two forests in persistence of suitable dung (see above) may account for the different periods of activity of these two coprophages in the two environments. The third abundant coprophage, *Aphodius* sp. #3, occurred only in the dry season in both forests (see Fig. 9).

Three saprophagous species common in both forests, *Rhyssemus germanus*, *Xylotrupes gideon* and *Phaeochrous emarginatus*, differ from each other in seasonal pattern of emergence (see Fig. 9), but have similar patterns of emergence in both forests.

Size Analysis. It has been postulated that insects grow larger in the longer growing season of tropical forests (SCHOENER & JANZEN, 1968). The two forests in the present study differ in minimum relative humidity, maximum temperature, and evaporation in ways that lead one to assume that the evergreen forest, which has more moderate temperatures and higher humidity has a longer growing season. It is appropriate to ask : Do the scarab beetles living in the evergreen forest achieve larger sizes than those in the deciduous forest? To answer this question two groups of species are considered separately: species that occur in both forests and species that are confined to one or the other forest. Species' mean lengths of every species in each group are compared between the two communities. Each trophic type is considered separately.

Table 7. Ranges and medians of mean lengths of scarab species at Sakaerat Experiment Station, northeastern Thailand.

	Dipterocarp Deciduous Forest			Dry Evergreen Forest		
	Herbivore	Coprophage	Saprophage	Herbivore	Coprophage	Saprophage
Species common to both forests						
Numbers of species	21	8	6	21	8	6
Ranges of means (mm)	4.9–21.0	3.0–12.3	2.0–32.9	5.2–21.5	3.8–11.3	2.0–43.0
Medians of means (mm)	9.9	4.7	6.7	10.0	4.1	7.2
Species confined to one forest						
Numbers of species	32	14	2	31	7	5
Ranges of means (mm)	4.0–21.0	2.0–19.0	9.0–12.0	5.0–36.5	3.0–15.0	21.0–46.0
Medians of means (mm)	7.3	4.5	10.5	14.0	4.0	26.0

Table 8. Tests of size differences between communities of scarab beetles at Sakaerat Experiment Station, northeastern Thailand.

	Herbivore	Coprophage	Saprophage
	Species common to both forests		
Pairwise tests[1]			
p =	>0.05	>0.05	>0.05
	Species confined to one forest		
Pairwise tests[2]			
p =	<0.100	>0.05	<0.05

1) WILCOXON matched-pairs signed-ranks test used for herbivores and coprophage: sign test used for saprophages because of small numbers of species.

2) MANN-WHITNEY U test used for all three trophic types.

Table 9. Size-frequency distribution of individual scarab beetles of species found in only one forest at Sakaerat Experiment Station, northeastern Thailand. Small beetles are more numerous in the deciduous than in the evergreen forest (KOLMOGOROV-SIMIRNOV, one-tailed test; $P<0.001$).

Size Class (mm)	Deciduous dipterocarp forest	Day Evergreen forest
1–3	63	18
4–6	281	58
7–9	224	79
10–12	21	33
13–15	3	20
16–20	21	39
21–25	4	19
26–30	0	0
31–35	1	1
36–40	0	8
41±	0	5
Total individuals	618	280
Total species	48	43

Table 10. Size differences between trophic types of scarab beetles within communities at Sakaerat Experiment Station, northeastern Thailand. P values of pairwise MANN-WHITNEY U tests.

	Deciduous Dipterocarp Forest	Dry Evergreen Forest
Saprophage-Herbivore	>0.4	0.09
Herbivore-Coprophage	0.001	<0.001
Saprophage-Coprophage	0.12	0.01

Species common to both forests The 35 species that occur in both forests (upper half of Table 7) allow us to test the effects of the two environments on intraspecific differences in size. Table 8 shows that for every trophic type none of the differences in species' mean lengths are statistically significant. Though intraspecific differences in means are slight and non-significant, the relative abundances of large and small species differ systematically. Figure 9 shows that four of the five abundant species that occur mainly in the evergreen forest are large species, while those six species that are more numerous in the deciduous forest are small species. Only one of the five species that are more abundant in the evergreen forest, *Apogonia sp.* #1, has lower mean length than any of the six "deciduous" species.

Species occurring in only one forest This analysis is a cross-specific comparison of insect sizes between the two communities with respect to mean lengths of "exclusive" species (lower half of Table 7). Table 8 shows that the herbivores and saprophages are larger in the evergreen that in the deciduous forest. But the coprophages show no singificant differences between communities. Table 9 shows the size frequency distribution of individuals of species confined to one forest. It is clear that smaller individuals are more numerous in the deciduous than in the evergreen forest.

Comparison of sizes of trophic types based on combined sample-sets of common and exclusive species (Table 10) shows that herbivores are significantly larger than coprophages in both forests. Saprophages are significantly larger than coprophages only in the evergreen forest.

Analysis of Diversity Patterns BRILLOUIN's (1956) formula was used in calculating diversity indices since it is a measure of the diversity of collections (PIELOU, 1966). The formula is :

$$H = \frac{1}{N}\left(\log_2 N! - \sum_{i=1}^{s} \log_2 n_i!\right)$$

where H is diversity per individual, N is total number of individuals, s is total number of species, and n_i is number of individuals in species i. Factors that mathematically affect the value of H are H, s and the relative abundances of the species (PIELOU, 1966).

Patterns of species diversity within trophic types provide no surprises. Seasonal trends of within-sample diversity (Fig. 10) seem to follow from the abundance and richness values given in Table 5. The parallel between the patterns for herbivores alone and those for combined samples (Table 11) appears to result from the dominant position of that type (see Table 5). The values of diversity within trophic types summed within seasons (Table 11) also parallel the abundance and richness values of Table 5. Species diversity in the deciduous forest is lower in the dry season than in either half of the wet season, whereas in the evergreen forest diversity in the dry season is intermediate between the values for the two halves of the wet season.

Thus, the analysis of species diversity shows that the dry season has a stronger inhibiting effect on the scarab community in the deciduous than in the evergreen forest, which is what we expect from the climatic conditions.

Pooling all samples across seasons (Table 11, last column), we find the diversity (H) and evenness (J) of distribution of individuals among species (PIELOU, 1969) of these two communities are similar.

It has been postulated that species diversity should be higher in an environment that is more predictable (SLOBODKIN & SANDERS, 1968). JANZEN & SCHOENER (1968) found higher diversity in Costa Rican insects in the less seasonal and more predictable environment of their study. According to this hypothesis diversity in Sakaerat scarabs should be higher in the evergreen forest than in the deciduous as the former is more predictable (INGER & COLWELL,). INGER & COLWELL have found higher diversity in reptiles and amphibians at Sakaerat in the evergreen forest (personal communication). However, the scarabs at Sakaerat do not support the hypothesis (Table 11). Herbivores and coprophages have higher diversity in the evergreen forest, as predicted by the hypothesis, but saprophages show higher diversity in the less predictable environment, the deciduous forest (Table 11). Very large numbers of a single species of saprophage in the evergreen forest may account for the departure from expectation of that trophic type. Eighty per cent (275/344)

of evergreen forest saprophages were *Xylotrupes gideon*. Species diversity for the combined samples is almost identical in the two forests.

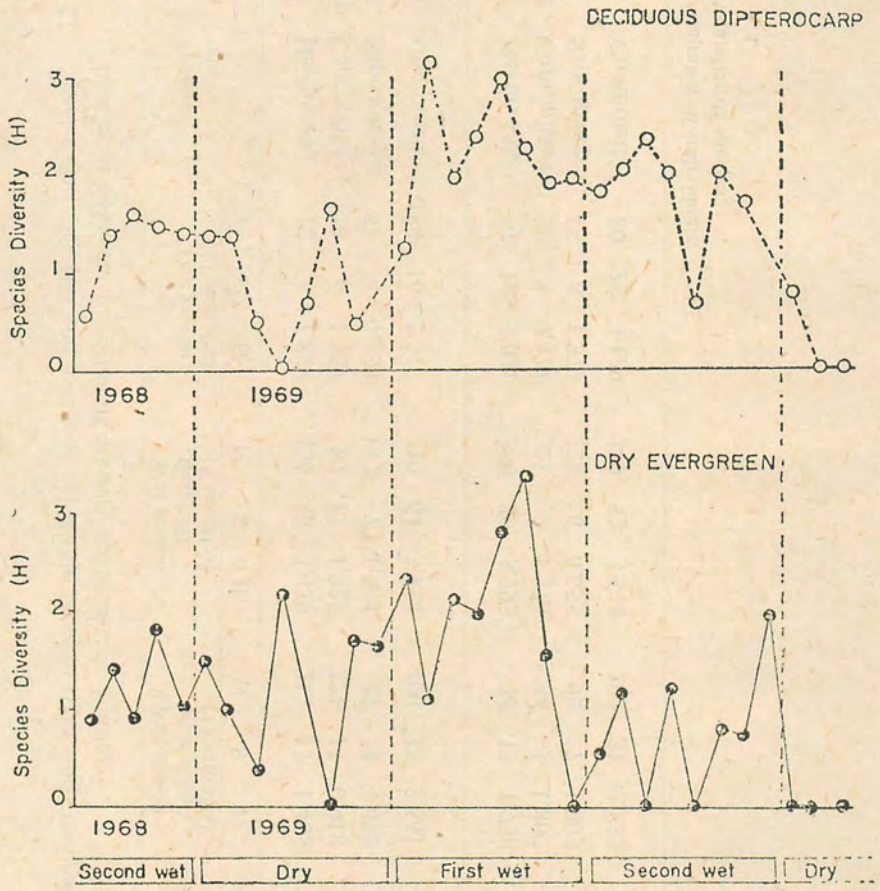


Figure 10. Seasonal variation of species diversity index (H) of scarab populations of all species in deciduous dipterocarp and dry evergreen forests at Sakaerat Experiment Station, northeastern Thailand.

Table 11. Species diversity (H) and evenness (J) within trophic types and combined samples of scarab beetles at Sakaerat Experiment Station, northeastern Thailand.

Habitats	Trophic types	Dry season (11 samples)			Wet season first half (8 samples)			Wet season second half (13 samples)			Sample spooled across seasons			
		N[1]	S[2]	H	N	S	H	N	S	H	N	S	H	J
Deciduous dipterocarp forest	Herbivores	12	6	1.888	486	46	3.439	212	13	1.465	710	53	3.471	0.60
	Coprophages	120	6	1.369	87	11	1.225	221	15	0.918	428	22	1.652	0.37
	Saprophages	52	4	0.580	137	7	1.344	47	4	1.482	236	8	1.975	0.65
	Combined	184	16	2.317	710	64	3.954	480	32	2.561	1,374	83	4.093	0.64
Dry evergreen forest	Herbivores	31	18	3.031	300	39	3.795	75	15	1.738	406	52	4.184	0.73
	Coprophages	31	4	0.474	21	7	1.573	34	9	1.807	86	15	2.036	0.52
	Saprophages	18	6	1.370	228	6	0.655	98	7	1.003	344	11	1.129	0.32
	Combined	80	28	3.129	549	52	3.574	207	31	2.833	836	79	4.065	0.64

1) N=number of individuals.
2) S=number of species.

DISCUSSION

The number of species in each forest is similar—83 species in the deciduous forest and 78 species in the evergreen forest. Of these, 35 species occur in both forests, yielding a low species overlap. Species overlap as measured by Horn's index is also very low.

Species diversity is almost identical in the two forests—4.093 in the deciduous and 4.065 in the evergreen. Size diversity is higher in the evergreen forest scarabs, which suggests that the foraging behaviour of vertebrate predators on these beetles may be more flexible in the evergreen forest than in the deciduous.

Three trophic types occur in both forests : herbivores, coprophages and saprophages: In terms of numbers of species the main difference between the two communities is the greater number of coprophages in the deciduous forest. In terms of numbers of individuals, the main differences are the greater numbers of herbivores and saprophages in the evergreen forest and the greater numbers of coprophages in the deciduous.

Of the species common to both forest, large species are relatively more abundant in the evergreen and small ones in the deciduous. In terms of species found in only one forest or the other, both herbivores and saprophages are larger in the evergreen forest than in the deciduous. Since coprophages as a group are the smallest scarabs in this set of samples, there is an interaction between the trophic types and sizes of beetles in these forests.

The greater abundance of large species in the evergreen forest may be related to differences in the lengths of the growing season. In the deciduous forest most beetles probably have developmental stages shortened because of decreasing soil moisture in the dry season. The more rigorous physical conditions of the deciduous forest may directly affect insect physiology by shortening the length of the larval period. Indirectly, they may affect insects by limiting availability of food, at least for herbivores and saprophages. In the evergreen forest the difference in soil moisture between the wet and the dry season is probably less severe because of the shading of the soil by the trees, the lower ambient temperature, and the lower rates of evaporation.

The rigorous conditions of the deciduous forest may thus select for smaller species. If energy sources (foliage and moist decaying plant material) are available for only short periods of time, it may be advantageous to allocate reproductive effort among many small individuals each with relatively short time necessary for maturation (SCHOENER & JANZEN, 1968).

The food supply of larvae of herbivorous and saprophagous species is particularly susceptible to decreases in soil moisture. Larvae of herbivorous species feed mainly on roots. Root-feeding larvae should be especially strongly influenced by the rigors of the dry season, which effectively stops movements of nutrients in the trees (Paul ZINKE, personal communication). This could be a signal causing larvae to stop feeding and pupate.

The interaction between climate and food availability probably does not control size in the coprophages. One might think that dung should last longer in the deciduous than in the evergreen forest, permitting adult coprophages to make larger dung balls in the deciduous forest and therefore providing for increased growth. But this is apparently not the case, as there are no significant size differences between environments in this trophic type. Once the adult has formed a dung ball and oviposited, the food supply for the larvae is restricted. The only thing that counts is the size of the dung ball in which they are growing. Therefore, on the basis of these ecological implications, differences in mean lengths between communities are less likely.

Coprophages are clearly the smallest among the three trophic types of scarabs, probably because the size of the food masses available to larvae are much more limited than plant roots and piles of decaying vegetative materials are to herbivore and saprophage larvae, respectively. In general, immature stages in coprophages are far shorter than those in herbivores and saprophages (HALFFTER & MATTHEWS, 1966).

The two forests differ in density of woody vegetation and the pattern of leaf fall. The greater density of vegetation and the evergreen habit of the trees in the evergreen forest provide a continuous and abundant supply of food for herbivores and saprophages. The more open nature of the deciduous forest makes it a hotter and drier environment, which probably holds dung of vertebrates in a more suitable condition for coprophagous scarabs for longer periods of time.

The same differences in vegetation account for a stronger seasonal climatic pattern in the deciduous forest. In turn this probably is responsible for the strong seasonal pattern in the species diversity of herbivores and saprophages and, especially, in the total abundance of herbivores.

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Appendix I

Distribution of samples from light traps used in analysis of scarab beetles from Sakaerat, northeastern Thailand.

Sample number	Sample date	Sample number	Sample date
1	9–10–68	17	5–16–69
2	9–24–68	18	5–20–69
3	10– 8–68	19	6– 4–69
4	10–18–68	20	6–13–69
5	11– 7–68	21	7– 6–69
6	11–28–68	22	7–11–69
7	12– 5–68	23	8– 9–69
8	12–12–68	24	8–12–69
9	1– 9–69	25	9–22–69
10	1–32–69	26	9–26–69
11	2– 5–69	27	10–17–69
12	2–27–69	28	10–21–69
13	3– 5–69	29	11–11–69[a]
14	3–13–69	30	11–21–69[b]
15	4–11–69	31	12– 9–69
16	4–29–69	32	12–26–69

a) Sampling date in evergreen forest is 11-8-69.

b) Sampling date in evergreen forest is 11-14-69.

Appendix II

Systematic species list with frequencies of individuals in each sample in two forest types in northeastern Thailand. First number in each pair is sample number as given in Appendix I. Second number is number of individuals in that sample.

	Deciduous dipterocarp forest	Subtotal	Dry evergreen forest	Subtotal
LUCANIDAE;				
Aegus kandiensis	12–1; 25–1	2	3–1; 25–1	2
Caleodes elegans		0	30–2	2
C. mouhoti		0	2–2; 4–1; 27–1	4
Dorcus biplagiatus	21–1	1	18–1; 19–1; 20–1; 22–1	4
D. buddha		0	17–1; 19–1	2
Nigidious sp. #1		0	13–1	1
PASSALIDAE:				
Leptaulax bicolor		0	2–1; 4–1; 9–1; 19–1; 29–1	5
Macrolinus andamanensis	18–1	1	14–1	1
SCARABAEIDAE:				
Ochodiinae:				
Ochodaeus sp. #1	3–2; 5–4; 6–2; 15–1; 18–9; 21–3; 24–1; 25–2; 27–2	26	3–1; 9–1; 25–2	4
Hybosorinae:				
Phaeochrous emarginatus	14–5; 15–30; 16–19; 17–1; 18–26; 19–12; 20–3; 22–1	97	9–1; 15–12; 16–3; 18–1; 19–12	29
Dynastinae:				
Alissonotum rangunense	7–1; 16–1; 19–1	3		0
Eophileulus chinensis		0	2–1	1
Eupatorus siamensis		0	14–1; 28–2	3
Heteronychus sp. #1	16–1	1		0
Oryctes cf. *desertorum*		0	6–1	1

Appendix II. – Continued

	Deciduous dipterocarp forest	Subtotal	Dry evergreen forest	Subtotal
Xylotrupes gideon	2–4; 15–10; 17–3; 18–4; 19–1; 21–1; 22–1; 24–1; 25–2; 27–8; 28–6	41	2–32; 4–6; 15–169; 16–2; 17–16; 18–4; 19–2; 20–2; 21–1; 22–2; 23–1; 25–17; 26–6; 27–11; 28–4	275
Euphirinae:				
Pronomacrous parryi		0	19–1	1
Geotrupinae:				
Balbochronus plagiatus	28–1	1		0
Kolbeus coreanus	12–2; 15–2; 18–1; 19–1; 25–1; 27–2	9		0
Aphodiinae:				
Aphodius sp. #1		0	19–2; 29–5	7
#2	6–1; 30–5	6	31–1	1
#3	5–2; 6–28; 7–7; 8–38; 9–1; 11–1	77	5–18; 6–2; 7–15; 8–10; 9–1	46
#4	15–1	1		0
#5	14–3; 19–1	4		0
#6	18–1; 21–2; 22–1; 23–1	5	19–1	1
#7		0	5–1	1
#8	25–1	1		0
#10	17–1; 24–1; 26–2; 27–4; 28–5	13		0
#11		0	9–1	1
#12	18–1; 19–1	2	19–1	1
#14		0	19–1	1
#15	20–1	1		0
#16	22–1	1		0
#17	4–1	1		0
Pleurophorus caesus	6–2; 7–1	3	5–1; 6–2; 8–1	4

Appendix II.–Continued

	Deciduous dipterocarp forest	Subtotal	Dry evergreen forest	Subtotal
Rhyssemus germanus	3–6; 6–40; 7–1; 8–1; 10–2; 11–1; 15–1; 16–1; 21–3; 22–1; 23–3; 25–3; 30–1	64	5–7; 6–4; 7–6; 8–1; 25–2	20
Coprinae:				
Copris corpulentus	4–1	1		0
C. doriae	6–1; 24–1	2	19–1; 29–1	2
C. furciceps	5–1; 6–1; 7–1; 8–2; 18–1; 23–1	7	16–1; 17–1; 18–1; 25–1	4
C. cf. *indicus*		0	29–1	1
C. sp. #1	23–1	1		0
Onthophagus sp. #1	1–1; 2–84; 3–7; 4–2; 5–10; 12–31 16–4; 17–42; 18–10; 19–4; 20–6; 21–2; 22–10; 23–37; 24–12; 25–7; 26–2; 27–10; 28–8; 30–1	290	3–2; 4–1; 14–2; 16–6; 17–2; 18–1; 19–1; 27–1; 29–1	17
#2	19–1	1		0
#3	23–1; 25–1	2		0
#5		0	23–1	1
#6	18–1	1	6–1	1
#7		0	23–1	1
Gymnopleurus melanarius	23–1	1		0
Rutelinae:				
Peltonotini:				
Pletonotus nasutus	15–5	5	17–3; 18–2	5
Anomalini:				
Anomala sp. #1		0	12–1; 13–; 14–3; 15–1; 19–4	14
#2	15–54; 17–2; 18–3	59	9–1; 15–1047; 16–15; 17–42; 18–12; 19–17; 20–1	1135

Appendix II. – Continued

	Deciduous dipterocarp forest	Subtotal	Dry evergreen forest	Subtotal
Anomala #3		0	17–1; 18–1; 20–1	3
#5	18–1	1	15–21; 17–1; 18–3; 19–5	30
#6		0	9–1; 19–2	3
#7		0	29–1	1
#8		0	14–1; 15–6; 17–2; 19–1	10
#9	19–1	1		0
#10	8–1	1	7–1	1
#12	15–1	1		0
#14		0	19–1	1
#19	18–1	1		0
Adoretini:				
Adoretus sp. #1		0	15–1; 16–1; 18–1; 19–1	4
#2	16–2	2		0
#3		0	19–1	1
#4		0	15–1	1
#5	15–2; 16–1	3		0
#6	15–1	1		0
#7		0	16–1; 18–1; 19–1	3
#8		0	9–1; 15–2; 16–2	5
#9	17–1	1		0
#11	17–1	1	4–1	1
#12	7–1	1		0
#14	17–43; 18–41; 19–7; 20–1	92		
Melolonthinae:				
Apogonia sp. #1	2–1; 15–1; 17–1	3	2–2; 12–1; 13–2; 14–4; 15–1; 17–2; 18–6; 19–1	19
#2	18–1	1	17–2	2

Appendix II. – Continued

	Deciduous dipterocarp forest	Subtotal	Dry evergreen forest	Subtotal
Apogonia #3	15–1	1		0
#4	16–1; 18–2	3		0
#5	2–138; 3–5; 4–2; 16–1; 18–12; 23–1; 24–2; 27–2; 28–2	165		0
#6	18–3	3		0
#7	15–43; 16–3; 17–10; 18–2; 22–1	59		0
#8	15–1	1		0
#9	4–1; 23–1	2		0
#10	18–1; 23–1	2		0
#11		0	15–5; 19–1	6
#12		0	29–1	1
Phyllophaga sp. #1		0	15–4	4
#2		0	9–2; 15–3; 17–2; 19–1	8
#3		0	12–1; 15–2	3
#4		0	15–2	2
#6	17–1	1		0
#7	15–11	11	5–3; 17–1; 19–1	5
#8		0	19–1	1
#9	15–1; 18–4	5		0
#10	15–2	2		0
#13		0	15–13	13
#14	15–1	1		0
#15	14–1	1		0
#16	15–2; 18–1	3		0
#17		0	15–1	1
#18	15–3	3	15–1	1
Cyphochilus proximus	2–2	2	1–2; 24–6; 4–3	51

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